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ALKANONES AND TERPENES IN THE MANDIBULAR GLANDS OF *ATTA* SPECIES (HYMENOPTERA: FORMICIDAE)*

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Abstract—1. The mandibular gland secretions of six species of ants in the genus *Atta* contain two ketones, 2-heptanone and 4-methyl-3-heptanone. The ratios of 4-methyl-3-heptanone : 2-heptanone vary from 2·4 : 1 in *Atta robusta* to 1 : 88 in *Atta laevigata*.

2. *Atta sexdens* produces geraniol and both isomers of citral in its mandibular gland. Both *Atta laevigata* and *Atta capiguara* contain citronellol in their glandular secretions.

3. 4-Methyl-3-heptanone functions as a releaser of alarm behavior in *Atta laevigata* and *A. sexdens* whereas 2-heptanone is not excitatory for either of these species.

INTRODUCTION

IN THE last decade, significant progress has been made in the analysis of the mechanisms of chemical communication among insects. Not surprisingly, this development has paralleled the advances made in the identification of the natural products which are employed by insects to transmit information. Because social insects utilize a variety of products as exocrine secretions, these arthropods have proven to be an especially rich source of compounds which are behaviorally active. Indeed, among the ants, nearly thirty natural products have been identified and at least one-fourth of these compounds have been demonstrated to be releasers of social behavior (Cavill & Robertson, 1965). At the present time, all of the identified ant-derived compounds which are classified as pheromones, the natural products biosynthesized in exocrine tissues, function as chemical stimuli of alarm behavior.

Alarm pheromones produced by ants originate in one of two glandular sources, the anal glands or the mandibular glands. The compounds synthesized in the anal glands, structures which are found only in members of the subfamily Dolichoderinae, are primarily terpenes and include a number of novel products which contain cyclopentanoid monoterpene nuclei (Cavill & Hinterberger, 1960). The mandibular gland constituents produced by species in the Myrmicinae, the largest of the ant subfamilies, have been scarcely investigated. Many genera in this diverse subfamily produce alarm pheromones in their mandibular glands, and although the chemistries of only four members have been studied, it is evident that the genera are capable of synthesizing a wide variety of natural products. Aliphatic carbonyl compounds are employed by species in two unrelated genera as alarm pheromones (Bevan *et al.*, 1961; McGurk *et al.*, 1966). On the other hand, the acyclic terpene citral is reported to be the alarm releaser in *Atta sexdens rubropilosa* Forel, a member of the most highly evolved of the myrmicine genera (Butenandt *et al.*, 1959).

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In 1963, one of us (M.S.B.) studied alarm behavior in populations of *Atta sexdens* in Peru. When either a crushed head or an excised mandibular gland was presented to workers, a typical sequence of reactions occurred among workers which were near the alarm stimulus. Almost immediately, the head and thorax were elevated and the mandibles were opened. The rate of ambulation increased markedly while the excited workers described unoriented circular movements which often resulted in collisions with their sister workers which in turn exhibited the same behavioral patterns.

Citral, on the other hand, caused none of these stereotyped reactions and thus it was evident that this terpene was not the mandibular gland constituent which triggered the release of alarm behavior. As a consequence of this fact, we undertook a comparative study of the chemistry of the mandibular gland complexes produced by six species of *Atta* in an effort to identify the alarm pheromones. The results of this investigation demonstrated that *Atta* species produce a wide diversity of natural products in their well developed mandibular glands.

MATERIALS AND METHODS

Insect material

Five of the species used in this investigation were collected in the State of São Paulo, Brazil. Extracts were prepared from heads of major workers representing the following species: *Atta sexdens* (L.), *A. laevigata* (Fr. Smith), *A. robusta* Borgm., *A. capiguara* Gonçalves and *A. bisphaerica* Forel. Living ants were decapitated and the heads were immediately transferred to methylene chloride. The extracted heads were shipped by air to the United States for subsequent chemical analyses. Workers of *Atta colombica* Guerin were collected from a laboratory colony maintained in the United States.

Analysis of mandibular gland components by gas-liquid chromatography

Extracts of the ant heads were filtered through sintered disk funnels which contained a 5 cm layer of anhydrous sodium sulfate. The extracts were dried over sodium sulfate for 24 hr and were concentrated to a small volume by vacuum evaporation at 30°C. The resulting concentrates were employed directly for gas-liquid chromatographic analyses on a Microtek 2000 gas chromatograph.

It was necessary to employ several stationary phases in order to resolve completely some of the mandibular gland components. An especially useful stationary phase for the low molecular weight oxygenated compounds was Chromosorb 102®. This styrene divinylbenzene copolymer served as both a stationary phase and a solid support and permitted the complete resolution of very closely related compounds. Fractionation of the highly volatile components in the mandibular gland secretion was achieved on a 6 ft glass column at an operating temperature of 250°C. Helium flow measured 60 ml/min and the resolved compounds were detected by a flame ionization detector. Quantitation of the identified constituents was effected by computing peak areas with a disk integrator mounted on the recorder.

Several other stationary phases with widely different polarities were employed in order to characterize the volatile components present in the mandibular gland secretions. Stainless steel columns (6 ft × ⅛ in.) containing the following liquid phases on 60–80 mesh Chromosorb W were utilized to fractionate the compounds present in the extracts of the heads: 20% Carbowax 20M, 10% FFAP® (reaction product between Carbowax 20M and 2-nitroterephthalic acid), 20% butanediol succinate (BDS), 5% Apiezon L, and 5% SE-30.

Fractionated components were collected for subsequent structural analyses by employing a splitter which permitted 90% of each component to by-pass the flame.

Infra-red absorption measurements were obtained on a Beckman IR-10 equipped with micro-cells. Methylene chloride was employed as an infra-red solvent.

Mass spectra of the mandibular gland components were obtained on a modified Consolidated 21–102 mass spectrometer. The inlet temperature was 100°C and high magnet runs were employed for most of the structural determinations.

RESULTS

Gas–liquid chromatography of the mandibular gland volatiles

Analyses on four different stationary phases indicated that all species of *Atta* contained the same two low boiling components. The infra-red spectra of both compounds demonstrated that they were simple open-chain ketones (Bellamy, 1964). Comparison of the retention times of the *Atta* compounds with a series of authentic ketones established that two alkanones, 2-heptanone and 4-methyl-3-heptanone, had retention times identical to those of the two ketones present in mandibular glands of the *Atta* species. The retention times of the authentic ketones and those of the two *Atta* compounds, on four different stationary phases, are presented in Table 1. The identical retention times of the two ketones in the *Atta* species with those of 4-methyl-3-heptanone and 2-heptanone on stationary phases of widely varying polarities indicates that the ant-derived ketones are the same as the two standards.

TABLE 1—COMPARISON OF THE RETENTION TIMES ON FOUR STATIONARY PHASES OF TWO AUTHENTIC KETONES AND TWO COMPOUNDS PRESENT IN *Atta* SPECIES

	Retention time (min)			
Compound	Chromosorb 102	BDS*	SE-30†	Apiezon L‡
2-Heptanone	6·4	4·3	2·1	1·6
Atta A	6·4	4·3	2·1	1·6
4-Methyl-3-heptanone	8·6	4·1	2·4	1·9
Atta B	8·6	4·1	2·4	1·9

* $T = 138°\mathrm{C}$ at a helium flow rate of 60 ml/min.

† $T = 105°\mathrm{C}$ at a helium flow rate of 60 ml/min.

‡ $T = 135°\mathrm{C}$ at a helium flow rate of 60 ml/min.

Although all species of *Atta* contain the same two alkanones, their ratios vary considerably between species (Table 2). In four of the six species, 2-heptanone is the major component, reaching an extreme in the case of *Atta laevigata* where it exceeds the branched alkanone by nearly ninetyfold.

TABLE 2—RATIOS OF 4-METHYL-3-HEPTANONE : 2-HEPTANONE IN SIX *Atta* SPECIES

Species	Ratio 4-Methyl-3-heptanone : 2-heptanone
Atta bisphaerica	1 : 7
Atta capiguara	1 : 2·6
Atta colombica	1·5 : 1
Atta laevigata	1 : 88
Atta robusta	2·4 : 1
Atta sexdens	1 : 4

The mandibular glands of all species contained higher boiling components which were fractionated readily by gas–liquid chromatography. Sufficient material was collected from three of the *Atta* species for structural analyses. The major components which were isolated had distinct terpene-like odors, which were easily detected if either a single head or a mandibular gland was crushed. Comparison of the retention times of a series of terpenes indicated that at least one terpene was present in each of the three species surveyed. The comparative retention times of standard terpenes and the compounds present in the *Atta* species are presented in Table 3.

TABLE 3—COMPARATIVE RETENTION TIMES OF STANDARD TERPENES AND COMPOUNDS PRESENT IN THREE SPECIES OF *Atta*

Compound	Retention time (min) Carbowax 20M*†	Retention time (min) FFAP*‡
Neral	4·5	14·6
Atta sexdens A	4·5	14·6
Geranial	5·2	15·3
Atta sexdens B	5·2	15·3
Geraniol	6·6	17·3
Atta sexdens C	6·6	17·3
Citronellol	5·1	11·2
Atta laevigata A	5·1	11·2
Atta capiguara A	5·1	11·2

* Conditions for the analyses of neral, geranial and geraniol: $T = 131$°C, He = 80 ml/min.

† Conditions for the analysis of citronellol: $T = 163$°C, He = 60 ml/min.

‡ Conditions for the analysis of citronellol: $T = 130$°C, He = 66 ml/min.

At least four different acyclic terpenes are present among the species of *Atta*, but unlike the qualitative consistency found in the case of the two alkanones, no common terpene denominator characterizes all species. Although not enough material was present in the extracts of *Atta bisphaerica* and *A. colombica* to characterize the higher boiling compounds, analysis of *A. robusta* demonstrated that none of the simple terpenes were detectable.

In *Atta sexdens*, the two isomers of citral, neral and geranial, constitute nearly 95% of the volatiles present in the mandibular glands of this species. Geranial is the major stereoisomer of citral, accounting for about 64% of this terpene. Geraniol on the other hand, is a trace constituent of the mandibular gland complex. In both *Atta capiguara* and *A. laevigata*, citronellol is the major terpenoid and citral is not present in detectable amounts.

Infra-red spectra of mandibular gland constituents

The infra-red spectra of the two low boiling components present in the mandibular glands of all *Atta* species were characteristic of open-chain saturated ketones (Bellamy, 1964). The spectrum of 4-methyl-3-heptanone was completely congruent with that of one of the *Atta* volatiles and that of 2-heptanone with the other.

The two main volatiles in the mandibular glands of *Atta sexdens* both exhibited strong absorption bands at 6·01 μ, indicative of a carbonyl function. The existence of a well defined band at 3·71 μ, characteristic of an aldehydic stretching vibration (Bellamy, 1964), demonstrated that these two compounds were aldehydes. The spectrum of citral was superimposable on those of these two aldehydes, identifying these two compounds as the stereoisomers of citral.

A distinct rose-like odor was associated with the high boiling component present in the head of *Atta sexdens*. The spectrum of this compound exhibited strong bands at 2·98 μ and 10·05 μ, both vibrations being characteristic of alcohols. The absorption at 2·98 μ is in the low range for a primary alcohol, and indicated that this compound was strongly hydrogen bonded. The complete congruency of the spectrum of this compound with that of the primary alcohol genaniol, conclusively identified this compound.

The major volatile component present in both *Atta capiguara* and *A. laevigata* also had a rose-like odor. Like geraniol, this compound possessed a strong absorption band at 2·98 μ but the OH deformation was present at 9·46 μ instead of 10·05 μ, as in geraniol. The superimposition of the spectra of this alcohol and that of citronellol established its structure unequivocally.

Mass spectra of the Atta *volatiles*

The mass spectrum of the first compound fractionated on Chromosorb 102 had a parent mass of m/e 114. This compound had a base peak at m/e 43 and a peak of moderate intensity at m/e 58. The latter peak is characteristic of aliphatic ketones which yield a rearrangement fragment which is equivalent to the lower molecular weight ketone, 2-propanone (Sharkey *et al.*, 1956). The presence of a moderate peak at m/e 71 represents the hydrocarbon fragment (C_5H_{11}) of the ketone which therefore must be a heptanone. The spectrum of 2-heptanone (Blum *et al.*, 1963) was congruent with that of the *Atta* constituent.

The second compound isolated by distillation on Chromosorb 102 had a parent mass at m/e 128 and as in the case of 2-heptanone, an intense peak at m/e 71 which can correspond to a C_5H_{11} fragment. Additional intense peaks at m/e 29, 57 and 86, indicated that the compound was a branched ketone, since the rearrangement peak at 58, characteristic of unbranched ketones, was absent. The fragment at m/e 57 can correspond to a $CH_3CH_2C{=}O$ moiety, and the fragment at 29 the alkyl portion of this fragment. These data were consistent with those of a branched 3-heptanone. The intense peak at m/e 86 must correspond to a fragment which contains a branched methyl group adjacent to the carbonyl function. This compound therefore must represent 4-methyl-3-heptanone. The mass spectrum of this ketone (McGurk *et al.*, 1966) and the *Atta* compound were identical.

The mass spectrum of the high boiling compound present in *Atta sexdens* presented a base peak at m/e 69 with a rather intense peak at m/e 93. The parent mass was at m/e 154. Geraniol had a totally congruent mass spectrum (von Sydow, 1963) with that of the *Atta* terpene.

The main volatile in both *Atta capiguara* and *A. laevigata* exhibited a parent mass at m/e 156. A base peak was present at m/e 69 and intense peaks were present at m/e 41, 55, 67, 81 and 95. The mass spectrum of citronellol was completely consistent with that of the *Atta* volatile.

Behavioral investigations with the volatile compounds in Atta

All compounds were evaluated on mature field colonies of either *Atta sexdens* or *Atta laevigata*. The activities of the *Atta* volatiles were determined by placing cotton balls impregnated with a compound either on the ant trail or near the nest opening. The reactions of the ants were observed for up to 1 hr after their exposure to the treated cotton balls.

In the case of both species, the reactions to 4-methyl-3-heptanone were immediate and dramatic. The ants exhibited typical alarm behavior, spreading their mandibles and elevating their thoraces and heads while they ran frenetically in circles, often colliding with their sister workers. When ants which were carrying leaves over their heads neared the ketone-treated sources, they dropped their cargoes and displayed typical alarm behavior. If the ketone was placed on the trail, activity was so disrupted that workers ceased moving away from the nest area and one-way traffic returned to the nest, bypassing the ketonic source.

In contrast, 2-heptanone was only mildly repellent and never produced alarm behavior. Within minutes after this ketone was presented to the ants, normal two-way traffic on the trail was evident and often the ants removed the ketonic source with little hesitation.

None of the terpenes was demonstrably active when assayed against the ants. At high concentrations all of these acyclic monoterpenes were somewhat repellent to the workers but in no case did these compounds cause any disruption of the normal activities of the ants.

DISCUSSION

The consistent occurrence of both 4-methyl-3-heptanone and 2-heptanone among species in the genus *Atta* indicates that these two alkanones are characteristic natural products of this genus. There are four subgenera in this genus (Borgmeier, 1959) and the six species surveyed in this investigation represent three of these subgenera. Although both of these ketones have been identified in other species of Hymenoptera, their occurrence is so sporadic that at this juncture no apparent phylogenetic significance can be attributed to their presence in members of a taxon.

4-Methyl-3-heptanone has been isolated also from six species in the ant genus *Pogonomyrmex*. Like *Atta*, this genus is a component in the subfamily Myrmicinae. However, *Pogonomyrmex* is a rather primitive genus in this subfamily whereas *Atta* probably represents the most highly evolved subfamilial genus. We have examined species in ten other genera in the Myrmicinae, representing a wide phylogenetic panorama of this subfamily, and 4-methyl-3-heptanone could not be detected in any members. Indeed, a species of *Trachymyrmex*, a genus which is in the same tribe as *Atta*, lacks this branched alkanone. The presence of hexen-2-al in the mandibular glands of a species of *Crematogaster* (Bevan *et al.*, 1961), a member of another genus in this large subfamily, indicates that a variety of aliphatic carbonyl compounds may be encountered among the taxa in this ant group.

Atta is the first genus in the Myrmicinae whose members have been demonstrated to produce 2-heptanone. Members of two genera in the Dolichoderinae, a more highly evolved subfamily of ants whose members characteristically biosynthesize terpenoid ketones, are rich sources of 2-heptanone (Blum *et al.*, 1963; Blum & Warter, 1966). The isolation of 2-heptanone from the honey bee *Apis mellifera* L. (Shearer & Boch, 1965) demonstrates that this methyl ketone is not limited to ants in its insect distribution.

The presence of three acyclic terpenes in the mandibular glands of *Atta* species extends considerably the distribution of terpenoids among the ant subfamilies. Citral had been isolated previously from *Atta sexdens* (Butenandt *et al.*, 1959) but neither citronellol nor geraniol have been reported to be present in any other members of the Myrmicinae. On the other hand, species in the most highly evolved of the ant subfamilies, the Formicinae, appear to be a rich source of these monoterpenoids. Citral, as well as citronellal, has been isolated from workers of *Acanthomyops claviger* (Roger) (Chadha *et al.*, 1962) and citronellol has been reported to be present in males of three species of *Lasius* (Law *et al.*, 1965). Since terpenes are known to be produced by species in four subfamilies of ants, this class of volatile natural products may play a key role in their social biologies.

If the function of 4-methyl-3-heptanone as a releaser of alarm behavior in *Atta* seems clearly established, the role of its ketonic congener seems especially cryptic. 4-Methyl-3-heptanone is also the alarm pheromone produced by *Pogonomyrmex* species, which parsimoniously employ this ketone as an attractant as well as a releaser of attack or digging behavior (McGurk *et al.*, 1966). Similarly, 2-heptanone is a potent releaser of alarm behavior in two species in the Dolichoderinae which produce this ketone in a specialized exocrine gland. The species of *Atta* which we examined behaviorally utilize the branched ketone as an alarm pheromone and we are unable to attribute any obvious communicative function to 2-heptanone. In four of the six species examined, 2-heptanone is the dominant ketonic species, exceeding 4-methyl-3-heptanone by nearly ninetyfold in the case of *Atta laevigata*. Another ant, *Tapinoma nigerrimum* Nyl., also produces two ketones in a single gland (Trave & Pavan, 1956), but unlike the case for *Atta* species, both of these carbonyl compounds, 2-methylhept-2-en-6-one and 2-methylheptan-4-one, release alarm behavior in a species in this genus (Wilson & Pavan, 1959).

Since 2-heptanone is employed by other ants as an alarm pheromone, the insensitivity of *Atta* to this ketone seems especially significant. The volatilities of 4-methyl-3-heptanone (b.p. 159°C) and 2-heptanone (b.p. 151°C) are similar, and both of these ketones would appear to be behavioral equivalents on the precedential grounds just cited. *Atta* species obviously exhibit a high degree of olfactory resolution and their exaggerated behavioral response to the branched ketone as opposed to the unbranched alkanone probably reflects the ability of ants to discriminate selectively the chemicals in their environment, a prerequisite to the development of an information transfer system based on specific volatile compounds. Ultimately, 2-heptanone may be demonstrated to function simply as a defensive secretion, along with the acyclic monoterpenoids which are present also in the mandibular gland secretions.

The structural simplicities of the *Atta* ketones may be deceptive from a biosynthetic standpoint. 4-Methyl-3-heptanone, as a natural product, is known only from the ant genera *Pogonomyrmex* and *Atta*. No simple biogenetic pathway can be postulated for the synthesis of this ketone, although the occurrence of its closely related concomitant 4-methyl-3-heptanol (McGurk *et al.*, 1966), is suggestive of its oxidative origin from an equally unusual natural product. Surprisingly, 2-heptanone derives its status as an animal natural product solely by virtue of its presence in ants and the honey bee. This ketone is also found in coconut oil (Allen, 1965), peppermint oil (Nagasawa, 1959) and is produced by various species of *Aspergillus* and *Penicillium* (Gehrig & Knight, 1961). These fungi can convert caprylic acid to 2-heptanone and it is postulated that the ketone can be formed by β-oxidation of the fatty acid followed by decarboxylation (Umeda & Hatano, 1949). Whether 2-heptanone is formed in ants by a similar pathway remains to be established. Nevertheless, even at this early stage in the study of the natural products chemistry of ants, the fact seems inescapably conclusive that these insects represent a rich source of organic compounds which are both structurally and biosynthetically provocative.

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